DISJUNCTION AND ENDEMISM IN CROTON ALABAMENSIS

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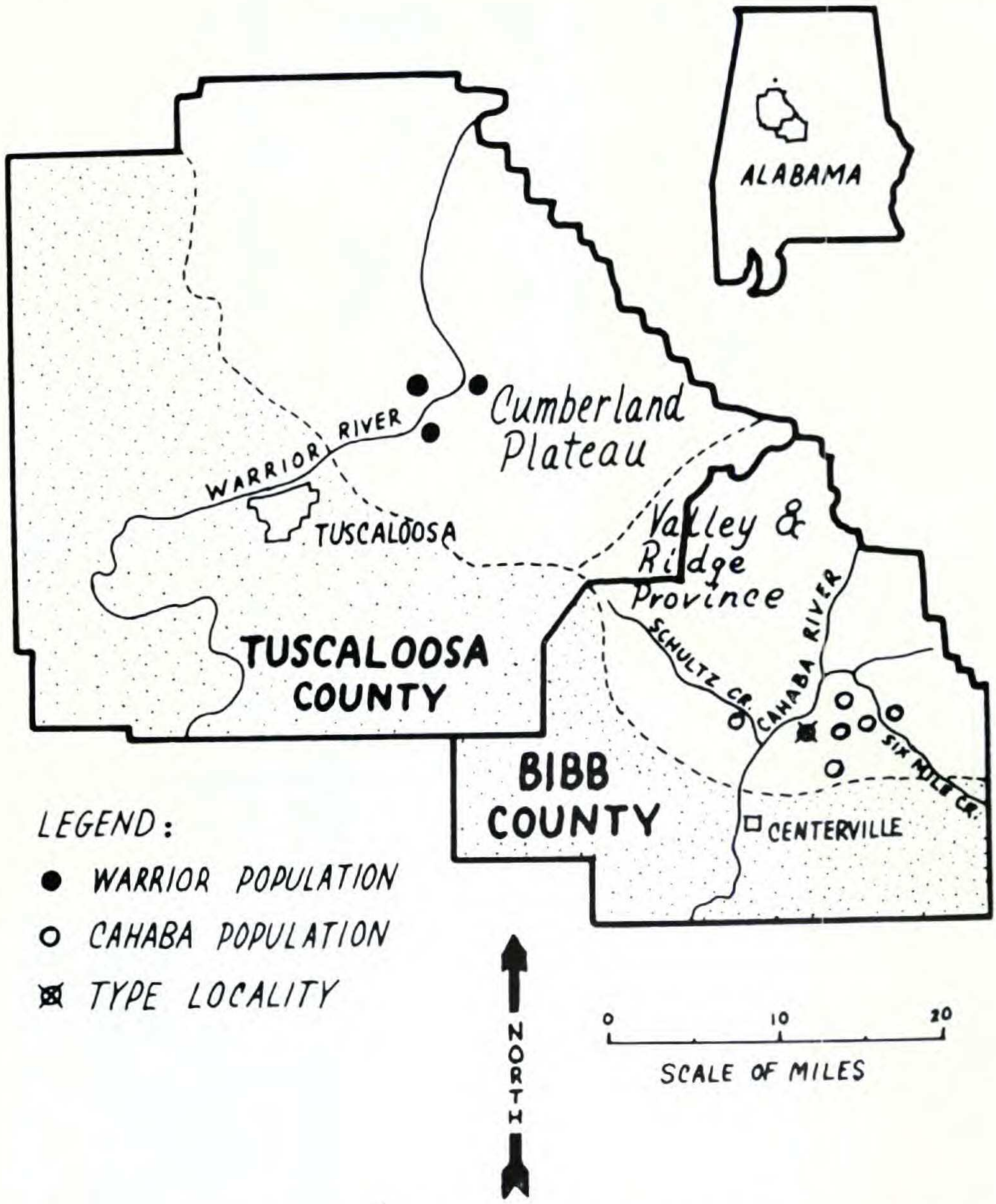
Croton alabamensis E. A. Smith *ex* Chapman is one of the rarest shrubs in the United States. It is known from two river valleys in central Alabama and is very narrowly distributed within this area (Map I). In the Herbarium of the University of North Carolina there is one sheet of *Croton alabamensis* which is reported from Tennessee. The label data on this sheet is as follows: Tullahoma, Coffee County, Tennessee, *T. G. Harbison 725*, Aug. 10, 1899. There is no other known record of this species outside of Alabama, and due to the very distinctive appearance of the plant at all seasons of the year it is unlikely that this species occurs in Tennessee at the present time. However, anyone doing field work in the vicinity of Coffee County should certainly be on the lookout for this rare plant. The species was first discovered in 1877 by Eugene A. Smith along the Cahaba River in Bibb County, Alabama. In 1905 Dr. Roland Harper found it along the Warrior River in Tuscaloosa County. Since that time the known range has been extended very little (Farmer, 1962). The species is now known from ten sites occupying something less than 100 acres irregularly distributed over about 30 square miles; about 25 square miles in the Cahaba River drainage, and about 5 square miles in the Warrior River drainage. Within these limited areas the species forms dense thickets giving the superficial appearance of one or more large clones, but no evidence of asexual reproduction of any kind has been found in this species.

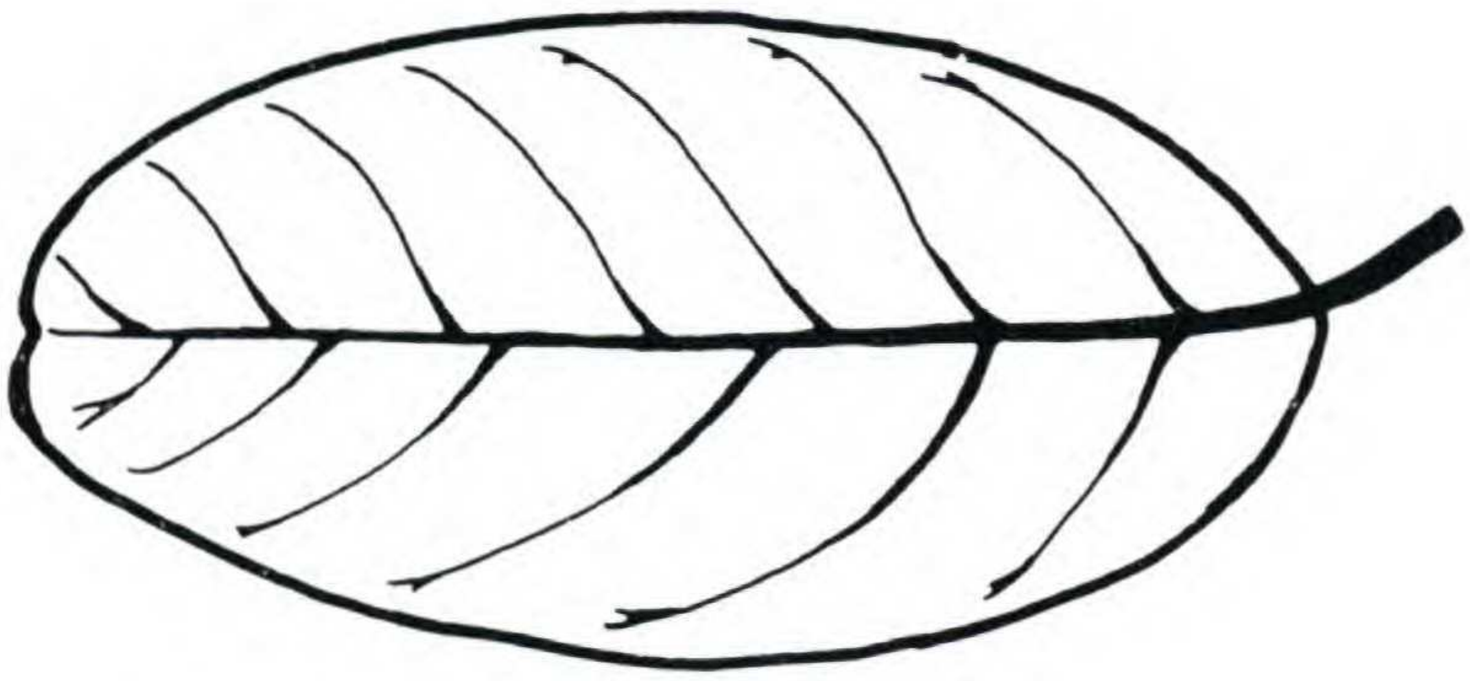
The distance between *Croton* sites on the Warrior and the nearest site on the Cahaba is approximately 25 air miles. This distance is apparently sufficient to prevent gene exchange between the populations in the two areas even in this wind pollinated species. Thus *Croton alabamensis* is particularly unusual in that it combines narrow endemism with



Map I. The distribution of *Croton alabamensis*. The stippled area represents Coastal Plain. Note that the distribution of this species is near, but always above, the Fall Line shown in dashes.

a disjunct distribution. In addition there is an interesting variation pattern both within and between the disjunct populations. The Warrior population differs from the Cahaba population in several morphological characteristics, and there is some evidence that they differ physiologically as well.

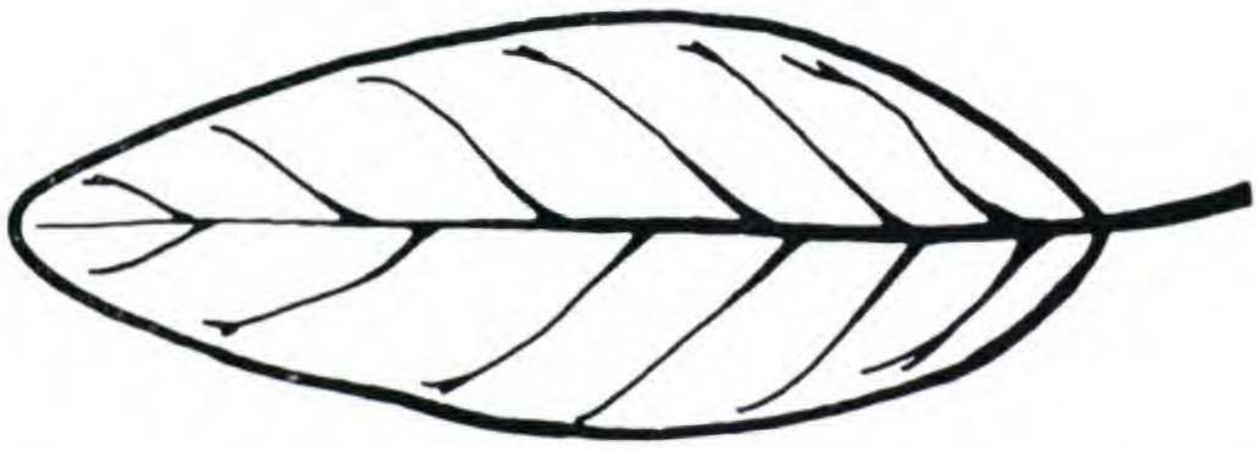
A.



TYPICAL LEAF OF WARRIOR POPULATION

1. Elliptical form
2. Emarginate apex
3. Average size: 37 ± 9.5 (50) mm by 80 ± 19.7 (50) mm

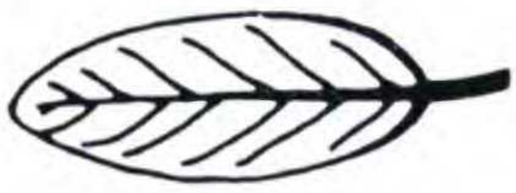
B.



TYPICAL LEAF OF CAHABA POPULATION

1. Ovate form
2. Acute apex
3. Average size: 25 ± 7.5 (50) mm by 66 ± 18.9 (50) mm

C.



TYPICAL LEAF OF PLANTS OF THE CAHABA POPULATION CHARACTERIZED BY UNUSUALLY SMALL LEAVES

Average size: 10.4 ± 2.47 (14) by 24.6 ± 7.18 (14) mm

Fig. I. Leaf variation in *Croton alabamensis*.

VARIATION BETWEEN WARRIOR AND CAHABA POPULATIONS

Mature plants of *Croton alabamensis* vary in height from about 1/2 to 3 1/2 m averaging about 1 1/2 m. In the Warrior population the mature shrubs average about 20% taller than those in the Cahaba population. Several differences are apparent in the size and shape of the leaves (Fig. I). The average leaf blade size for Warrior plants is 37 ± 9.5 (50) mm. The largest single leaf found in this population measured 75 by 170 mm. For the Cahaba population the plants can be divided readily into two categories based on leaf size as indicated in Fig. I. Most of the plants are like those indicated by B in Fig. I, where the average size was 25 ± 7.5 (50) mm by 66 ± 18.9 (50) mm; whereas for the fewer, extremely small-leaved plants, (Fig. I C) the average leaf size was found to be only 10.4 ± 2.47 (14) mm by 24.6 ± 7.18 (14) mm. Leaf shape in the Warrior plants also differs consistently from that of Cahaba plants. Leaves of Warrior plants are elliptical with an apex which varies from slightly to distinctly emarginate; those from Cahaba plants are more ovate with an acute apex which is not emarginate.

Reproductive structures also show a consistent size difference between plants from the two river valleys. Flowers, fruits and seeds from Warrior plants are approximately 20% larger than those from Cahaba plants. It was also observed that in the Cahaba population relatively more branches bear predominantly pistillate inflorescences, as compared with approximately equal numbers of staminate and pistillate inflorescences found on Warrior plants. Normal time of first flowering for the species is within the first two weeks of March, but Cahaba flowering usually precedes Warrior flowering by about a week. Erratic occurrence of a few flowers at almost any time of year is not uncommon but was observed to occur with greater frequency among Cahaba plants.

CYTOLOGY

Previously it was thought that the plants from these two river valleys differed in chromosome number, the Warrior

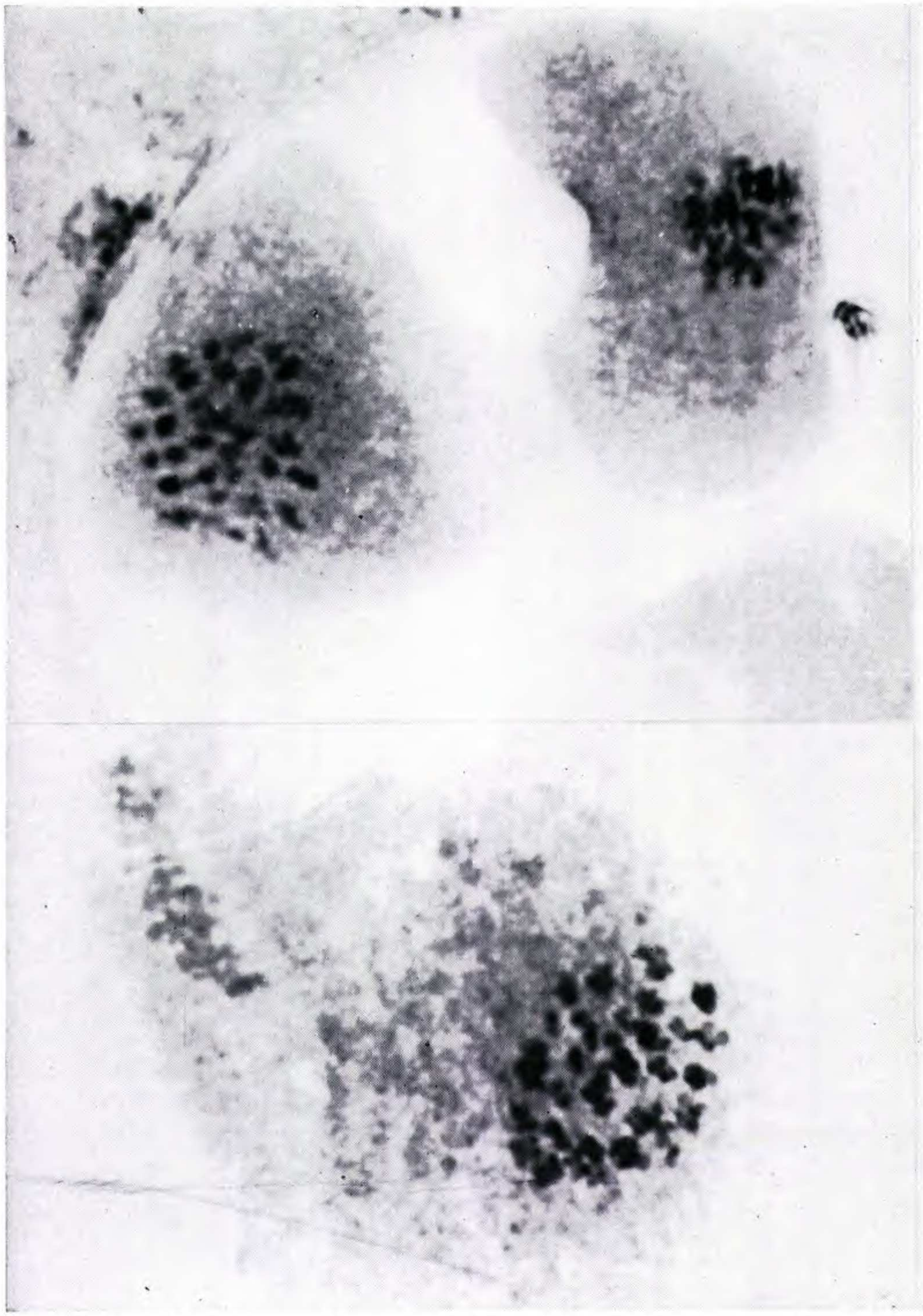


Fig. II. Metaphase II configurations of the two populations of *Croton alabamensis*. Above, Cahaba population; below, Warrior population.

material having $n = 32$, the Cahaba material $n = 16$. (Farmer 1962, Webster 1967). This correlated very nicely with the size differences noted above. Recent studies have shown that the situation is not that simple. During February and March 1968, chromosome counts were made on 15 different individuals from the Warrior population, and 18 different individuals from three different sites in the Cahaba drainage. The latter included individuals representing most of the morphological variation described above. All of the individuals examined from both populations were found to have the number $n = 32$. This is not to imply that the original counts were in error, although no 16-chromosome plants were found in this survey of 33 individuals from four different sites. The authors are convinced that at least the Cahaba populations contain individuals with the number $n = 16$ as well as individuals with $n = 32$, although the latter number apparently occurs with much greater frequency. The lower chromosome number previously reported for Cahaba material was seen in both mitotic and meiotic divisions. The mitotic counts were made on radicles of germinating seeds, the meiotic counts on pollen mother cells. The counts made during the spring of 1968 were primarily on pollen mother cells, although one count from each river system was made on root tips of softwood cuttings. Voucher specimens of three individuals from each population counted are deposited in the herbarium of the University of Alabama. For the Cahaba population the voucher specimens are *Joab L. Thomas #1615, 1616, 1617*; for the Warrior population, *Joab L. Thomas #1628, 1629, 1630.*

Meiosis appeared to be normal in all of the material examined. Diakinesis was rarely seen in this material, but when this stage was encountered bivalent pairing was evident and no clear multivalent formations were seen. The chromosomes of *Croton alabamensis* are very small, and there is considerable size variation within the chromosome complement. Correlated with a difference in flower size noted between Warrior and Cahaba material, bud size and

anther size at the time of meiosis is approximately 20% larger in Warrior material than in Cahaba material. For this reason, and perhaps for others, Warrior material was much easier to work with, and it was always easier to find division figures in this material.

An interesting relationship was noted between division synchrony and weather conditions at the time the material was collected. Generally, in material collected during an unusually cold period a high degree of asynchrony was seen, whereas material collected a day or two following a short warm period would invariably show more synchrony.

HABITAT

A brief description of the habitat of *Croton alabamensis* is particularly interesting and relevent because an equally rare species, *Neviusia alabamensis* has recently been found growing along side the *Croton* in one small area along the Warrior River. The habitat consists of moderately-to-steeply-sloping terrain with shallow soil derived from and underlain by sandstone, shale, or limestone. The area is also characterized by high soil and air temperature and intense drought during the summer. During late summer, in particular, extreme drought is a common feature of the rock-outcrop habitat. The relief of the Warrior and Cahaba areas is similar. Elevations range mostly from 300 to 400 feet above sea level. The *Croton* thickets in the Cahaba drainage are mostly on gentle slopes of approximately 20 degrees and are usually facing south or southwest. Those of the Warrior area are found primarily on north-facing bluffs where the slopes are estimated at greater than 45 degrees (Fig. III). The difference in exposure is thought to be primarily responsible for the generally higher soil and air temperatures recorded in the Cahaba habitat. Also, in spite of the steep slope, the Warrior habitat usually has more soil moisture due to seepage through the shale. In both areas the thickets are usually found about midway up the slopes, seldom extending either to the top or to the base of the slopes.

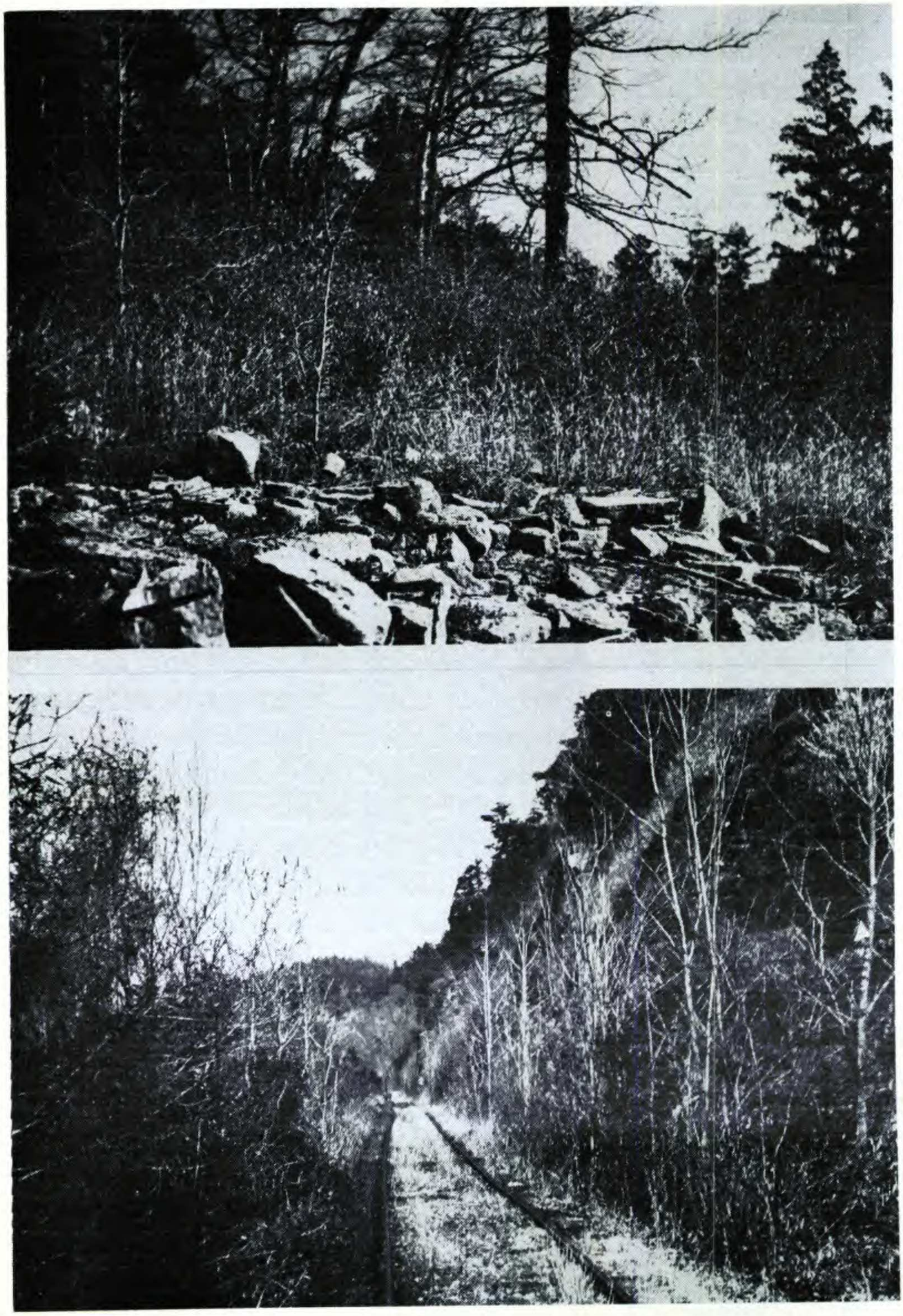


Fig. III. Habitats of *Croton alabamensis*. Above, Cahaba area; below, Warrior area.

Prominent outcrops of bare rock are visible throughout the area of both the Warrior and the Cahaba populations, but the rocks are of different geological ages and mineral composition in the two areas. The rocks of the Warrior area are primarily Pottsville shale and sandstone of the Pennsylvanian, whereas those of the Cahaba are mostly Ordovician limestone. Likewise soil pH shows some variation between the two areas, that of the Cahaba ranging from 6.5 to 7.8, that of the Warrior from 6.0 to 6.8.

Morphological and physiological characteristics of *Croton alabamensis* which apparently contribute to its survival in this habitat include the following. Flower buds develop and become well differentiated in late spring and are dormant before the beginning of summer extremes of drought and high temperature. The following spring the pre-formed buds flower and develop fruits rapidly, seed dehiscence usually being complete by the end of May. Heavy seed crops are produced each year, and the seeds are released by a catapult mechanism with adequate range to seed most of the available substratum. This is thought to be an important factor in maintaining the locally dense populations of *Croton*. Because of dormancy the seeds do not germinate until early the following spring. Young seedlings rapidly become established and enter dormancy early in the summer. In this manner the seeds and the seedlings survive the drought and high temperatures of late summer. Adaptations favoring moisture conservation within the plant during these extremes include: (1) stomata on the lower leaf surface only; with the stomata, both leaf surfaces, and the stems densely covered by scale-like, peltate trichomes; (2) drooping or wilted leaves during most of the daylight hours; (3) abscission of many of the leaves during late summer; and (4) general plant dormancy from mid-summer to early spring. The shallow rooting habit is correlated with shallow-habitat-soil and facilitates rapid water absorption following rains.

Thus the habitat factors which are apparently most critical in determining the distribution of this species are

the slope, the shallow soil over rock, and the high soil and air temperatures associated with middle and late summer drought. *Croton alabamensis* seems to be particularly well adapted to this apparently unfavorable habitat.

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